ON THE GROWTH OF THE ADULT COLONY OF POCILLOPORA BULBOSA

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WITH FOUR TEXT-FIGURES AND ONE PLATE

INTRODUCTION.

THE object of this investigation, which was started at the suggestion of Prof. Stephenson, was to observe in detail the method of growth of a mature colony of *Pocillopora* for comparison with the early development of the same form worked out by Prof. Stephenson. It was originally intended to study in particular the method of formation and growth of the new polyps by keeping living colonies under constant observation. Twelve small colonies of *Pocillopora bulbosa* were attached to concrete blocks 3 in. square, and the latter were fastened by wires to the inner walls of an open tub situated in the Western Moat (the natural habitat of the species) and always submerged. It was found, however, that growth was so rapid that it would have been necessary to examine the colonies at least every three days in order to follow the growth of individual polyps. Time did not permit of an examination being made more frequently than once a fortnight, and hence a record of the growth changes from month to month only is recorded, together with the observation of many isolated stages in polyp formation. Subsequent examination of part of the corallum of a colony whose growth stages had been followed proved of interest, as the relative ages of most of the corallites was known, and the relation between soft tissue bearing polyp buds in process of formation and the hard parts below could be ascertained.

PREVIOUS WORK.

The growth of entire coral colonies over periods of months and years has been investigated most recently by Mayor (1924) and Stephenson (to be published shortly in this volume). Mayor summarizes the previous published work on the subject, and records the increase in linear dimensions and in weight of *Pocillopora damicornis* var. *cespitosa*, *P. eydouxi* and *P. brevicornis* (1924, pp. 62, 66–67, and 71–72). Respecting the genus *Pocillopora* Gardiner remarks that, "The growth of the colony is much more vigorous towards the summits of the branches, and to this is due the angular character of the calices here and their very thin walls" (1897, p. 942). Increase in the number of corallites takes place

by gemmation, fissiparity being very rare (Duncan, 1885, p. 47). Accounts of the main types of development of the corallum in the Madreporaria are given by Ortmann (1890), von Koch (1896) and others, and multiplication of the soft parts has more recently been studied by Duerden (1902, 1903, etc.) and Matthai (1926), but none of these accounts deal with the Pocilloporidae. Many photographs and figures of the Pocilloporidae have been published, but they do not show the skeletal details of budding (Hoffmeister, 1925; Vaughan, 1907 and 1918 ; Dana, 1846, etc.), and the process is very briefly described by Milne Edwards (1860, p. 302). The present account gives for the first time details derived from a study of the living and growing colony.

GROWTH AND BUDDING OF POCILLOPORA.

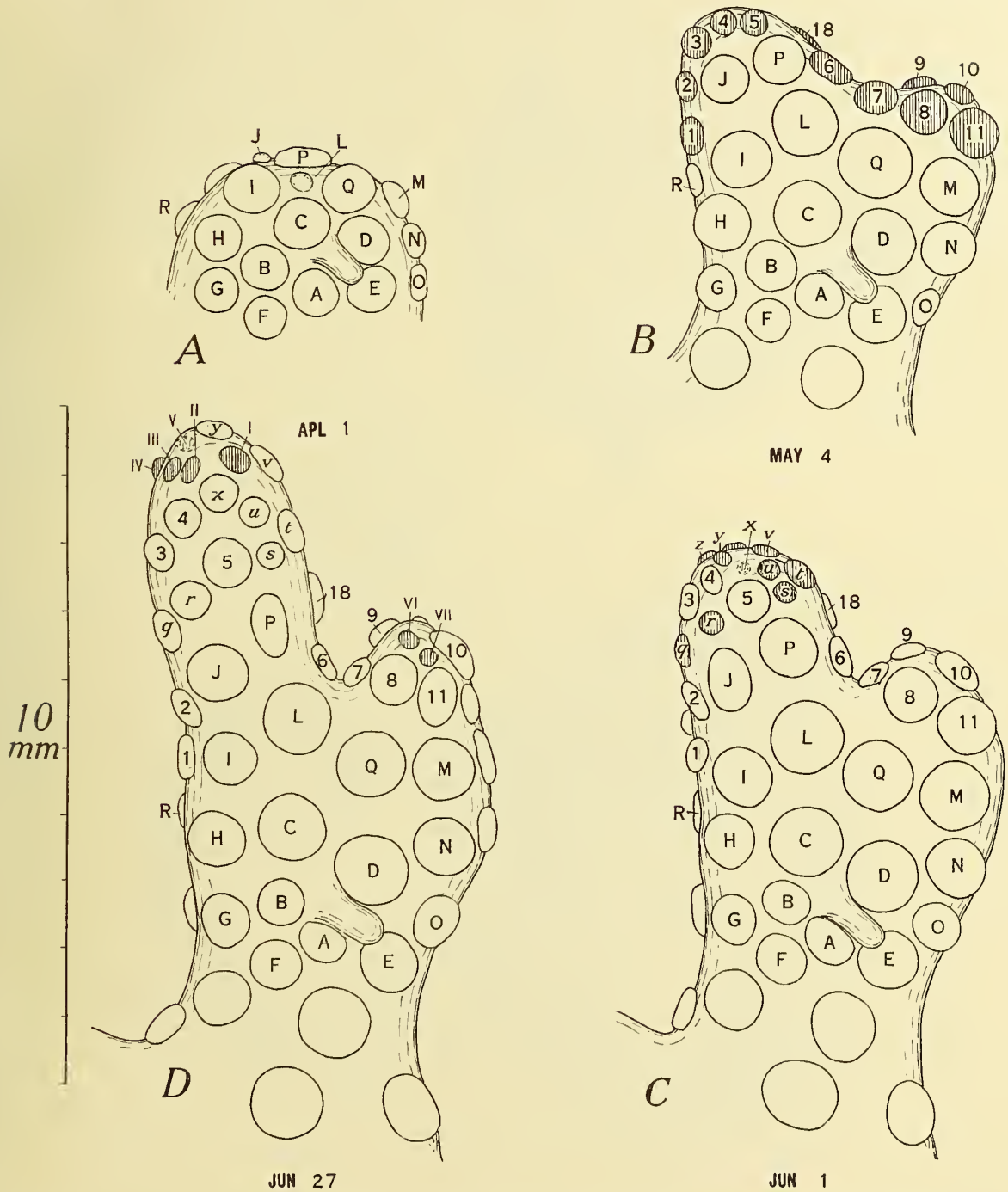
Text-figs. 1 and 2 record the changes undergone by the terminal portion of a branch on an actively growing colony of *Pocillopora bulbosa*. The dimensions of the colony were about 5 × 3·5 cm. and 2·5 cm. high. At the side of one branch, 2 mm. from the tip on 1st April, a solid knob-like outgrowth projected bearing no polyps, and this abnormality served as a recognizable fixed point of reference for subsequent growth. The diagrams in Text-fig. 1 show the positions of the polyps on the branch in side view, new polyps formed during the previous month being cross-hatched. When viewed from above on 1st April the branch appeared as indicated in Text-fig. 2, *A*. The polyps were moderately expanded in diffuse light; in strong sunlight they contracted within the calix.* In mature polyps the twelve tentacles are of almost equal length. Mesenteries were not always clearly visible through the tissues.

By 4th May considerable growth had taken place, and when the same branch was viewed from above, few of the original polyps were visible (see Text-fig. 2, *C* and *D*), and the projecting knob was no longer apparent from above. From Text-figs. 1, *A* and *B*, and 2, *A–D* it will be seen that the increase in height above the knob from 2 mm. on 1st April to 4·8 mm. on 4th May has been accomplished by (1) the addition of new polyps situated in between the old ones at the tip (in Text-fig. 1, *D*, old polyps are marked A, B, C, etc., new polyps 1, 2, 3, etc.), and (2) by the spreading out and divergence of the polyps already present. The branch had also widened considerably at the tip and showed signs of becoming bifid, a furrow extending across it (Text-fig. 2, *C*).

After another month's growth the branch became definitely bifid, but one branchlet was much longer than the other, and bore numerous new apical polyps (Text-fig. 1, *C*, *q*, *r*, *s*, etc., cross-hatched). The second branchlet had been formed mainly by upward and outward growth of the original corallites, only one new polyp appearing at the apex, and not visible in side view (Text-fig. 1, *C*). Growth of the lower polyps had continued to a slight extent, polyps L and Q, etc., being further from the knob. The tip of the longer branchlet now measured 6·2 mm. from the knob.

By 27th June the longer branchlet extended 8 mm. beyond the knob and had increased greatly in size by both the above-mentioned methods, the new polyps lying in between the old ones at the tip (Text-fig. 1, *D*, and 4, *A*, I, II, III, etc., hatched). The shorter branchlet had grown slightly and showed three new apical polyps. The main axis of the branch below the bifurcation had not elongated, and polyps L, Q, etc., remained at the same distance from the knob and from each other.

* This applies to certain colonies of *Pocillopora* only ; many will expand their polyps in full sunlight.



TEXT-FIG. 1, *A–D*.—Diagrams of the side view of a growing branch of *Pocillopora bulbosa*, showing the size of the branch and the positions of the polyps present on 1st April, 4th May, 1st June and 27th June respectively. Polyps appearing for the first time during the previous month are cross-hatched. Polyps of different ages are numbered or lettered as follows:

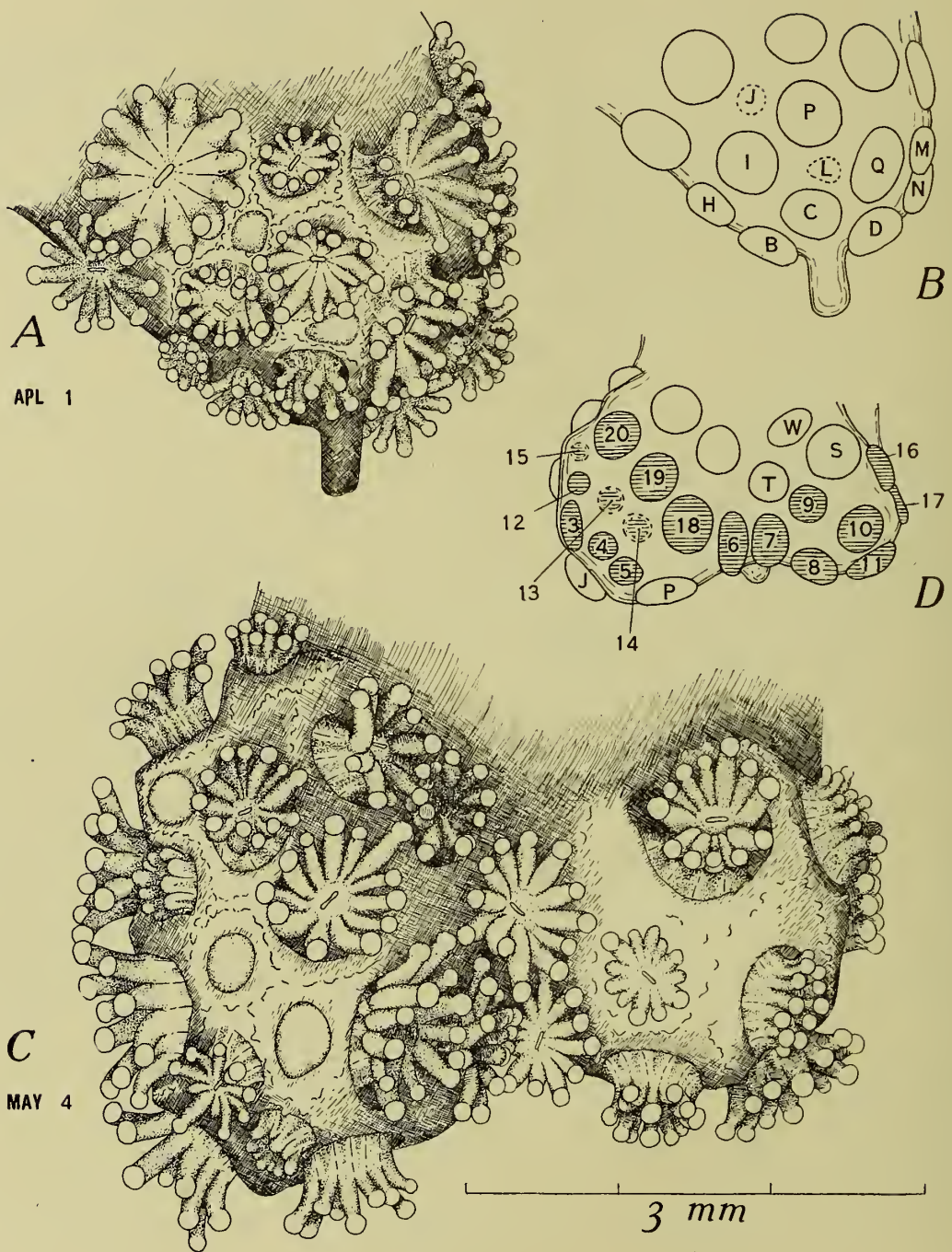
A, B, C, etc., polyps present on 1st April.

1, 2, 3, etc., new polyps formed between 1st April and 4th May.

a, b, c, etc., new polyps formed between 1st April and May 4th.

I, II, III, etc., new polyps formed between 1st June and 27th June.

The abnormal knob-like outgrowth which served as a fixed point for observing growth is seen in Text-figs 1, *A–D*.



TEXT-FIG. 2, *A* and *C*, show the appearance of the same living branch of *Pocillopora* when viewed from above on 1st April and 4th May respectively. The abnormal knob-like projection which served as a fixed point for observing subsequent growth is seen in Text-fig. 2, *A*. TEXT-FIG. 2, *B* and *D*, give a key to the lettering and numbering of the polyps seen from above on those dates; the diagrams are on the same scale as the side views of the branch seen in Text-fig. 1, *A* and *B*. The lettering and numbering is the same as for Text-fig. 1, where a key is given. For further description reference may be made to the text.

In 88 days the linear increase of the branch above the knob was approximately 6 mm., but very little increase in height occurred below it. Active growth in length is limited to the tips of the branches of the colony, but growth in thickness takes place everywhere. The growth rate of the branch under observation corresponds to an annual increase in height of 25 mm. Mayor records an increase of 7–28·5 mm. per annum for *Pocillopora damicornis* var. *cespitosa* in Pago Pago Harbour, and 37–61 mm. on the Aua line in Samoa. Thus it may be assumed that the colony under observation on Low Isles was healthy and growing at a normally rapid rate. It may be noticed that the linear growth-rate was not constant during the three months of observation, the increase per day being on an average 0·101 mm., 0·092 mm. and 0·069 mm. during the months of April, May and June respectively. The surface temperature of the sea during these three months gradually fell about 6·5° C., from 27·4° C. to 21° C. It is not clear from the insufficient data available whether the observed fall in growth-rate bears a direct and simple relationship to the fall of temperature, since it is possible that besides being influenced directly by temperature, a branch at different ages may normally grow at various rates.

FORMATION OF NEW POLYPS.

It has been seen that the formation of new polyps was restricted to the apex of the branch figured. On the entire colony polyp-formation occurs most rapidly at branch tips, and on the edge zone of the encrusting basal part of the colony. Some stages in the development of the soft parts of new polyps, as seen in surface view, are shown in Text-figs. 2 and 3. Polyps always arise by extra calicinal budding. The first indication of budding is seen in the appearance of a flat area of coenosarc between the existing polyps such as that lying between polyps 10, 16 and S in Text-fig. 2, *C* and *D*; three weeks later a fully-formed polyp occupied this situation. The corallum at such a stage already shows the beginning of the formation of the theca (see below). Budding may be much more rapid than this. For example, the space between polyps 5, 14, 18 and P seen in Text-fig. 2, *C* and *D*, gave rise to four fully-formed polyps during the following four weeks. The bud first appears externally as a convex circular area showing no external structure (Text-figs. 2 *A* and *C*, polyps J, L, 14 etc., 3, *B* and *C*). It then enlarges slightly, and pigmented stripes appear upon it corresponding in number with the tentacles and mesenteries. The stripes may alternate in size, and one larger than the rest may be formed at one side (Text-fig. 3, *C*). In other cases the pigmented stripes may be perfectly regular all round, and vary in number from about eight to twelve. Tentacles arise as bulges round the margin of the convex bud, and the mouth appears soon after tentacle formation has begun.

The details of tentacle formation here, unlike those in the very young colony (see Stephenson, 1931, p. 127), are very variable; but the adult polyps become almost similar, showing twelve sub-equal tentacles, or occasionally the directive tentacles slightly enlarged. The twelve tentacles may appear (1) almost simultaneously, or (2) the directive tentacles may arise first, followed by further tentacles appearing in couples, the directive tentacles remaining much larger than the rest for a considerable period. When twelve tentacles are formed together, large and small tentacles usually alternate, and the directive tentacles are not markedly larger than any other couple (Text-fig. 3, *B*, left-hand polyp, and 2, *C*, polyps 5, 12 and 9). Rarely eight or ten tentacles only may be formed together, but they similarly alternate in size; the polyps attain a large size

before the full number of tentacles is made up (Text-fig. 3, *B*, lower polyp). The dimorphism in tentacle size may be slight or very great, and persists till the polyp is nearly adult (Text-fig. 2, *C*, polyps 18, 19 and 20).

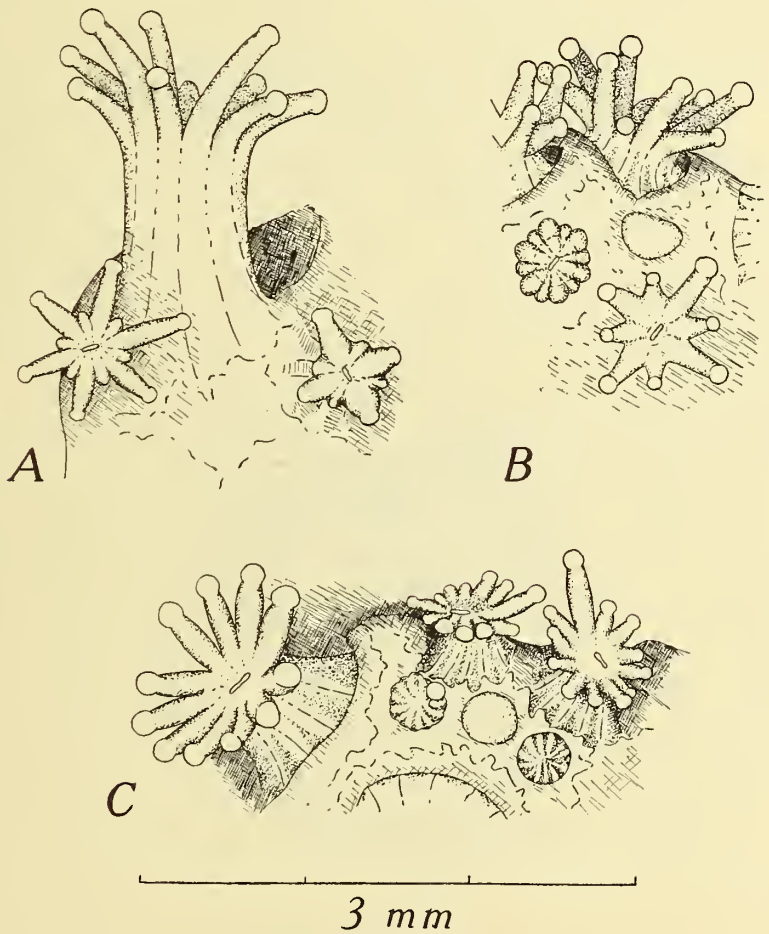
The colony shown in Text-fig. 3, *C*, shows one directive tentacle arising first and remaining much larger than the rest (two upper polyps), until the adult stage is reached (left-hand polyp), where the tentacles are practically equal. In such cases, where one or both directive tentacles arise first, they are followed either (1) by two large and three small couples, so that a regular alternation of large and small rudiments is formed (as in Text-fig. 3, *A*, left-hand polyp; the very young one on the right shows as yet the rudiments of one large and two small couples, besides the directive tentacles), or (2) by three large and two small couples. Where one directive tentacle is much larger than its fellow, the fifth (last) couple of tentacles to appear lies on either side of the second directive tentacle. Thus there is no constant order of tentacle formation in buds situated at the tips of branches, such as is seen in the early development of the entire colony, although the method apparent in adult colonies may be constant for the various parts of the same colony. A loss by the adult of the somewhat strict regularity of the early stages is a feature frequently met with in coelenterate development.

GROWTH OF THE CORALLUM.

After the colony had been examined on 27th June it was killed and the corallum cleaned (Plate I, fig. *A*). The history of all the apical corallites and of those over one side was known (see Text-fig. 1, *D* and 4, *A*). The youngest polyp rudiments visible externally in the soft tissue were v and XII (Text-fig. 1, *D* and 4, *A*). Polyp v had no mouth or tentacles, but pigmented stripes were present, and polyp XII appeared as a barely detectable convex area. Text-fig. 4, *B* shows a drawing from above of the skeleton at the tip of the longer left-hand branchlet; a satisfactory photograph of such a curved surface could not be obtained. Polyp v, although lacking mouth and tentacles, is provided with a small but definite calix, about 0·2 mm. deep (Text-fig. 4, *B*). The walls of the calix are slightly fluted and smooth and very thin, a narrow common calicinal wall separating the cavity of the calyx from those adjacent to it. Below the youngest visible polyp rudiment lies a concave platform XII appearing on a level with the upper edge of the calices of three adjacent corallites. In the soft tissues of the living colony no polyp rudiments were visible between polyps v, x and IX, or between II, *x* and *y*, but the skeleton shows the initial stages of calix formation in these situations (Text-fig. 4, *B*, calices XIII and XIV).

The formation and growth of the calices in the adult *Pocillopora* appear to be as follows: At the tips of the branches the calices are crowded, so that there is a common narrow colline separating the cavities of adjacent calices. As the latter grow upwards and outwards in divergent directions, the free edge of the colline at the junction of two or three calices expands into a small flat area, as at XIII and XIV in Text-fig. 4, *B*. Shortly after this the polyp rudiment becomes visible externally, and growth of the edges of the calices converts the flat area into a concave hollow (Text-fig. 4, *A* and *B*, calix XII). Further growth of the colony results in the new calices becoming deeper, and at the same time wider as the older calices diverge from each other. Successive stages in this process are seen in calix v and in the slightly older calices I, IX, X and XI in Text-fig. 4, *B*, the latter being about 0·5 mm. deep, and less than three weeks old. The walls of these calices are now slightly

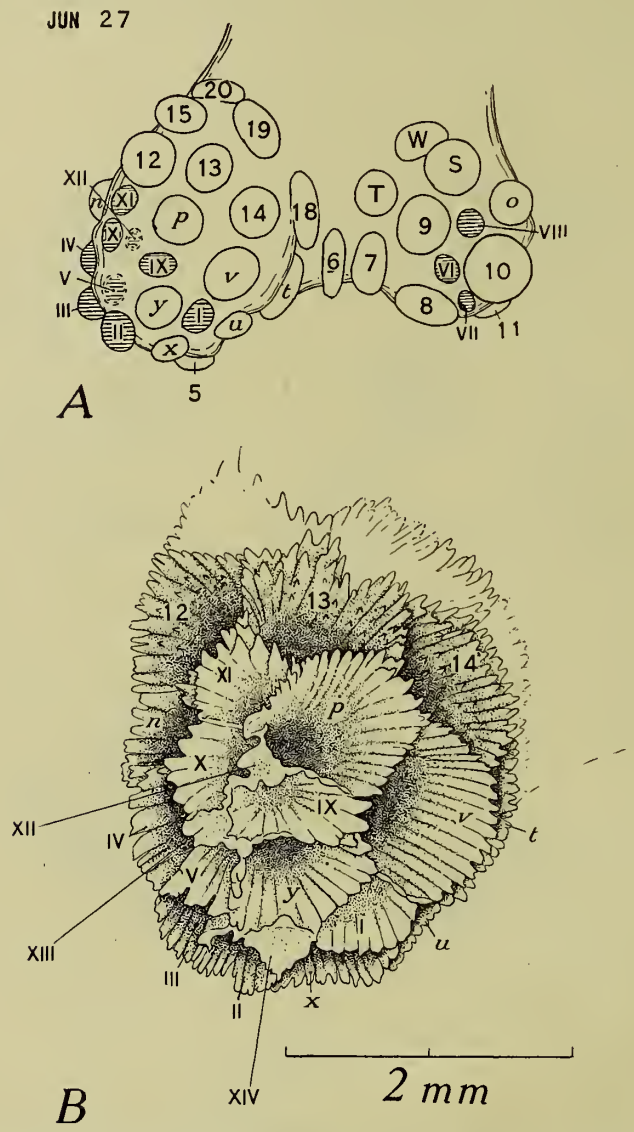
fluted, smooth and very thin. The surrounding calices *n*, *p*, *v* and *y* (Text-fig. 4, *B*, and 1, *D*) are older (less than six weeks), and are consequently deeper (1·2–1·5 mm.) and wider. Their cavities are V-shaped in section, with the bases very near together and lying below those of the younger polyps (Text-fig. 4, *B*); and they are united by a solid mass of skeleton formed by basal thickening of the calix walls. The collines are still sharp (Text-fig. 4, *B*, and Plate 1, figs. *A* and *B*, between calices VI and VII and between 8 and 11), and the calix fluted and smooth within.



TEXT-FIG. 3, *A*, *B* and *C*.—Showing the appearance of portions of living *Pocillopora* colonies where growth is rapid and new polyps are being formed. For a description of the stages here shown, reference may be made to the text.

Calices 12, 13 and 14 (Text-fig. 4, *B*, see also Text-fig. 2, *D* and 4, *A*), are about ten weeks old. They are slightly larger than calices *n*, *p*, *y*, etc., and their cavities have the same maximum depth, although a thicker solid axis now lies between them. The walls have thickened so that one or two spines now lie on the free edge, and the twelve septa can be detected as twelve rows of spines within the calix. The direction of growth of the calix, however, has been turned towards the tip of the branch to a slight extent, and has been more rapid on the side nearer the tip, so that this side of the calix tends to overgrow the younger ones beyond it, and the deepest part of the calix lies immediately within its

proximal rim. The septa thus radiate in a fan-shaped manner over the distal wall from the deep basal part of the calix within its proximal rim, while the septa on the proximal wall are short, and hardly seen in direct surface view, as they lie within the rim (see photograph in Plate I, fig. *A*, calices 8 and 11).



TEXT-FIG. 4, *A*, shows diagrammatically the positions of the polyps, as seen from above on 27th June, on the branch of *Pocillopora* under observation, which is figured in side view on this date in Text-fig. 1, *D*. A key to the lettering is given with Text-fig. 1. This view of the branch may be compared directly with those shown in Text-fig. 2, *B* and *D* on 1st April and 4th May respectively. TEXT-FIG. 4, *B* shows part of the corallum at the tip of the left-hand fork of this branch (see also Plate I, *A*, side view). The lettering of the calices is the same as that of the polyps in Text-fig. 4, *A*. For further description of the formation of the calices and their subsequent development, as seen in this figure, reference may be made to the text.

Later the calices grow more slowly, and tend to do so directly outwards, so that the linear increase of the branch almost ceases. Growth in thickness of the branch continues by thickening of the walls and bases of the calices. The calices thus become further separated. This is clearly seen in Plate I, fig. *A*, where the sharp ridge between calices

8 and II bears one row of spines, that between Q and M three rows of spines, and that between D and O three to four irregular rows of spines. At the base of the branch as many as six rows of spines lie between two calices. With the outward growth of the calices the axial mass of skeleton increases and the calices become shallower. Their bottoms become flattened instead of V-shaped in section, and lie less than 0·5 mm. below the surface (Plate I, fig. *A*, calices C, D, etc.). The walls stand almost at right angles to the bottoms, and the septa are nearly radially symmetrical instead of showing the peculiar early symmetry noticed above. On the upper parts of the colony a columella is scarcely apparent and directive septa may just be detectable. On the basal encrusting portions of the colony a papilliform columella may rise from the base of the calix to the surface level. Its formation starts very early, as soon as the calix appears at the growing edge of the base of the colony.

Increase in thickness of the axial skeleton of the branches, resulting in the restriction of the calices to the outer parts of the corallum, is accomplished near the tips by deposition of solid skeleton at the bases of the calices, but elsewhere by the formation of tabulae. They are formed particularly rapidly in the angles between the branches and on the lower parts of the branches. Such an area is shown in the photograph in Plate I, fig. *C*, the surrounding branches having been broken off to expose the part. A tabula arises as a thin ring of smooth calcite about 0·1 mm. or less in thickness, projecting directly inwards from the side walls of the calix. Further growth enlarges the flat projection, and reduces the central pore leading to the basal part of the calix. Finally the pore is closed and a horizontal tabula is completed, leaving a closed cavity towards the axis of the branch, and forming a slightly convex floor to the calix (Plate I, fig. *C*). The process is then repeated, so that a series of tabulae is formed one outside another, cutting off chambers about 0·3 mm. in depth. Spines situated on the inner walls of the calix remain enclosed in these chambers. Where growth in diameter of a branch is most rapid the calix walls are fairly thick, and grow up so fast that few spines are found upon them. A series of tabulae is formed independently in adjacent calices, the rings first appearing at about 0·2 mm. below the surface, and on completion the tabulae lie about 0·3 mm. below the surface (Plate I, fig. *C*). The calices are here much shallowed than on the distal parts of the colony not showing the formation of tabulae (Plate I, fig. *A*).

SUMMARY.

1. The growth of individual branches of *Pocillopora bulbosa* during three months was studied. The colonies under observation were kept in the sea and were growing normally.

2. Linear growth of the branches took place mainly by the formation of new polyps at the tips by extra-calicinal budding. Further down the branches growth took place by enlargement and separation of the corallites already present, together with the formation of tabulae; only occasionally were new polyps added here.

3. Details are given of the course of development of the polyps as seen externally in living material. Comparison may thus be made with the development of the young colony recorded by Stephenson (see Vol. III, No. 3 of these reports).

4. The mode of growth of the corallum is described, particularly the development of new calices and tabulae.

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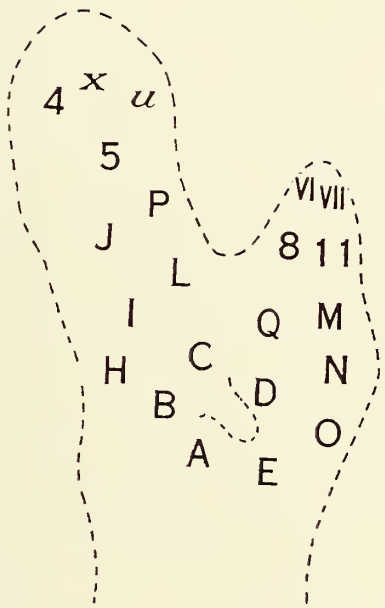
DESCRIPTION OF PLATE I.

FIG. *A* shows a photograph of the corallum on 27th June of the branch under observation and shown diagrammatically at various stages in Text-fig. 1. Fig. *B* gives a key to the numbering and lettering of the calices seen most clearly on the corallum and which can be compared with the side view of the living branch, Text-fig. 1, *D*, where the positions of the polyps are similarly marked. A key to the lettering and numbering is given with Text-fig. 1. Fig. *C* shows a photograph of the corallum at an angle between several branches, most of which have been broken off to expose the part more fully. This area shows tabulae being rapidly formed, and many are seen in various stages of development. For further description reference may be made to the text. $t._1$, tabula developing as a projecting shelf from the corallite wall. $t._2$, tabula nearly completed, the shelf being wider and the central space smaller. $t._3$, fully formed tabula, developed from a stage such as $t._2$ by obliteration of the central space. $t._4$, corallite split vertically, showing three successive tabulae.



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